Extremal dynamics model on evolving networks

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We investigate an extremal dynamics model of evolution with variable number of units. Due to addition and removal of the units, the topology of the network evolves and the network splits into several clusters. The activity is mostly concentrated in the largest cluster. The time dependence of the number of units exhibits intermittent structure. The self-organized criticality is manifested by a power-law distribution of forward avalanches, but two regimes with distinct exponents $\tau=1.98\pm0.04$ and $\tau'=1.65\pm0.05$ are found. The distribution of extinction sizes obeys a power law with exponent 2.32 ± 0.05 .

PACS numbers: 05.40.-a, 87.10.+e, 87.23.Kg

Extremal dynamics (ED) models [1] are used in wide area of problems, ranging from growth in disordered medium [2], dislocation movement [3], friction [4] to biological evolution [5]. Among them, the Bak-Sneppen (BS) model [5] plays the role of a testing ground for various analytical as well as numerical approaches (see for example [1,6–11]). The dynamical system in question is composed of a large number of simple units, connected in a network. Each site of the network hosts one unit. The state of each unit is described by a dynamical variable b, called barrier. In each step, the unit with minimum b is mutated by updating the barrier. The effect of the mutation on the environment is taken into account by changing b also at all neighbors of the minimum site.

General feature of ED models is the avalanche dynamics. The forward λ -avalanches are defined as follows [1]. For fixed λ we define active sites as those having barrier $b < \lambda$. Appearance of one active site can lead to avalanche-like proliferation of active sites in successive time steps. The avalanche stops, when all active sites disappear again. There is a value of λ , for which the probability distribution of avalanche sizes obeys a power law without any parameter tuning, so that the ED models are classified as a subgroup of self-organized critical models [12].

The BS model was originally devised in order to explain the intermittent structure of the extinction events seen in the fossil record [13]. In various versions of the BS model it was found, that the avalanche exponent is $1 < \tau \le 3/2$, where the maximum value 3/2 holds in the mean-field universality class. On the other hand, in experimental data for the distribution of extinction sizes higher values of the exponent, typically around $\tau \simeq 2$ are found [14]. The avalanche exponent close to 2 was also measured in ricepile experiments [15]. While there are several models of different kind, which give generic value

 $\tau = 2$ [16,17], we are not aware of any ED model with such a big value of the exponent.

The universality class a particular model belongs to, depends on the topology of the network on which the units are located. Usually, regular hypercubic networks [1] or Cayley trees [11] are investigated. For random neighbor networks, mean-field solution was found to be exact [18,7]. Also the tree models [11] were found to belong to the mean-field universality class. Recently, BS model on random networks, produced by bond percolation on fully connected lattice, was studied [19]. Two universality classes were found. Above the percolation threshold, the system belongs to the mean-field universality class, while exactly at the percolation threshold, the avalanche exponent is different. A dynamics changing the topology in order to drive the network to critical connectivity was suggested. Similar model was investigated recently [20] in the context of autocatalytic chemical reactions.

We present here a further step towards reality. In fact, one can find real systems in which not only the topology of connections evolves, but also the number of units changes. The network develops new connections, when a new unit is inserted, and if a unit is removed, its links are broken. This is a typical situation in natural ecologies, where each extinction and speciation event changes also the topology of the ecological network. The same may apply to economics and other areas, where the range of interaction is not determined by physical Euclidean space. This problem was already partially investigated within mean-field BS model [21] and also in several other models devised for description of biological evolution [17,22–24], which use different approaches than the extremal dynamics

The purpose of this Letter is twofold. First, to study the evolution of topology in a ED model with variable number of units. Second, to demonstrate that the large value of the avalanche exponent can be observed if the topology of the underlying network evolves dynamically.

We consider a system composed of varying number $n_{\rm u}$ of units connected in a network. In the context of biological evolution, these units are species. The dynamical rules of our model are the following.

- (i) Each unit has a barrier b against mutations. The unit with minimum b is mutated.
- (ii) The barrier of the mutated unit is replaced by a new random value b'. Also the barriers of all its neighbors are replaced by new random numbers. If b' is larger than barriers of all its neighbors, the unit gives birth to a new unit (speciation). If b' is lower than barriers of all neighbors, the unit dies out (extinction). As a boundary condition, we use the following exception: if the network consists of a single isolated unit only, it never dies out.

This rule is motivated by the following considerations. We assume, that well-adapted units proliferate more rapidly and chance for speciation is bigger. However, if the local biodiversity, measured by connectivity of the unit, is bigger, there are fewer empty ecological niches and the probability of speciation is lower. On the other hand, poorly adapted units are more vulnerable to extinction, but at the same time larger biodiversity (larger connectivity) may favor the survival. Our rule corresponds well to these assumptions: speciation occurs preferably at units with high barrier and surrounded by fewer neighbors, extinction is more frequent at units with lower barrier and lower connectivity. Moreover, we suppose that a unit completely isolated from the rest of the ecosystem has very low chance to survive. This leads to the following rule.

(iii) If a unit dies out, all its neighbors which are not connected to any other unit also die out. We call this kind of extinctions singular extinctions.

From the rule (ii) alone follows equal probability of adding and removing a unit, while the rule (iii) enhances the probability of the removal. As a result, the probability of speciation is slightly lower than the probability of extinction. The degree of disequilibrium between the two depends on the topology of the network at the moment and can be quantified by the frequency of singular extinctions. The number of units $n_{\rm u}$ perform a biased random walk with reflecting boundary at $n_{\rm u}=1$. The bias towards small values is not constant, though, but fluctuates as well.

(iv) Extinction means, that the unit is removed without any substitution and all links it has, are broken. Speciation means, that a new unit is added into the system, with a random barrier. The new unit is connected to all neighbors of the mutated unit: all links of the "mother" unit are inherited by the "daughter" unit. This rule reflects the fact that the new unit is to a certain extent a copy of the original, so the relations to the environment will be initially similar to the ones the old unit has. Moreover, if a unit which speciates has only one neighbor, a link between "mother" and "daughter" is also established.

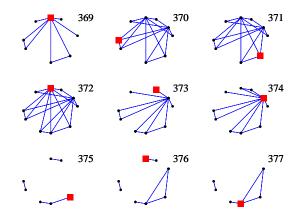


FIG. 1. An example of network configurations in several successive time steps, from step 369 to 377. Units are represented by small filled circles. The lines represent links between the units. The unit with the minimal barrier b is indicated by a filled square.

The above described rules are illustrated in Fig. 1. Speciation occurs in the transition from step 369 to 370, 371 to 372, 373 to 374 and 375 to 376. In the transitions from 372 to 373, 374 to 375 and 376 to 377 extinction occurs (last two include also singular extinctions). We can see that after speciation the neighbors of the new unit have one neighbor more than before, so that if $n_{\rm u}$ increases, also the connectivity of the network grows.

We investigated the evolution of the network by measuring time dependence of several quantities. We start the simulation with the initial condition $n_u=1$. A typical result is shown in Fig. 2, where we show the time dependence of the number of units $n_{\rm u}$, average connectivity \bar{c} , and the frequency of singular extinctions $f_{\rm s}$. The network can be split into disconnected clusters, as is illustrated in the Fig. 1. In Fig. 2 we show also the evolution of number of clusters in three size categories. We denote by n_1 the number of the smallest clusters, of size 2, by n_2 the number of medium-size clusters, larger than 2 and smaller or equal to $n_{\rm u}/2$, and by n_3 the number of clusters larger than $n_{\rm u}/2$. The value $n_3=1$ means that most of the system is concentrated in a single cluster.

We can see that singular extinctions occur in bursts. The passages without singular extinctions, where number of units evolves like a random walk (due to equal probability of increase and decrease of number of units by 1) are interrupted by short periods, where $n_{\rm u}$ falls to small values and singular extinctions are intense. We can see that very often three events coincide: high frequency of singular extinctions, large number of clusters, especially of size 2, and the fact, that the largest cluster does not contain most of the network. We observed, that the mu-

tation occurs nearly all the time in the largest cluster. A similar effect was reported also in the Cayley tree models [11]: the small isolated portions of the network are very stable and nearly untouched by the evolution.

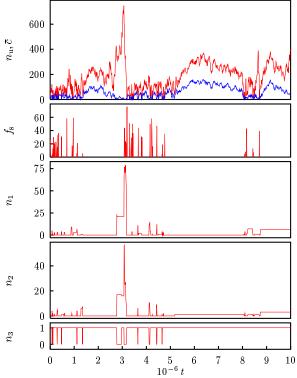


FIG. 2. Time evolution of quantities describing the size and topology of the network, in a typical run. From top to bottom: the number of units $n_{\rm u}$ (upper line) and average connectivity \bar{c} (lower line), number of singular extinctions during 10^3 steps, number of clusters of size 2, number of clusters of size larger than 2 and $\leq n_{\rm u}/2$, number of clusters of size larger than $n_{\rm u}/2$.

Figure 2 suggests that the number of units exhibits intermittent drops. This corresponds qualitatively to punctuated equilibria seen in the fossil data. This feature is new in our model, when compared with previous approaches within the BS model [21] but resembles the intermittent features of models based on neural networks [17], Lotka-Volterra equations [23], and coherent noise [22]. In order to check this property quantitatively, we plot in Fig. 3 the distribution of changes in number of units during time interval $\Delta t = 3 \cdot 10^4$ steps. We can see that the distribution of drops $(\Delta n_{\rm u} < 0)$ has a power-law tail, which confirms the intermittency.

The distribution of forward λ -avalanches [1] is shown in Fig. 4. We found power-law distribution for $\lambda_c = 0.016$ with the exponent $\tau = 1.98 \pm 0.04$. The value of the exponent was found by fitting the data in the interval $(500, 5 \cdot 10^5)$ [25]. Contrary to the BS and related models, we found power law distribution with a different exponent $\tau' = 1.65 \pm 0.05$ also for λ larger than about 0.4. (More precisely, we obtained the value of the exponent

by fitting the data in the interval (500, 10⁶) for $\lambda=0.4$ and $\lambda=0.6$. Both values of λ give the same result). The data suggest that for $\lambda>\lambda_c$ the avalanche size distribution exhibits two regimes, with crossover around certain avalanche size $s_{\rm cross}$. For small avalanches, $s< s_{\rm cross}$, the distribution is power law with exponent τ , while for larger avalanches, $s>s_{\rm cross}$, power law with exponent τ' holds. The crossover $s_{\rm cross}$ grows when λ approaches to λ_c .

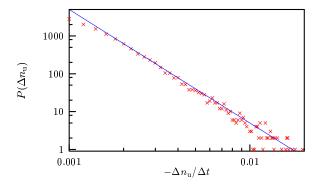


FIG. 3. Distribution of drops in number of units during the interval $\Delta t = 3 \cdot 10^4$ steps. The full line is a power with exponent -3.

The existence of avalanches for λ close to 1 is related to the fluctuation of the number of units. We observed, that such avalanches start and end mostly when number of units is very small. Between these events the evolution of the number of units is essentially a random walk, because singular extinctions are rare. This fact can explain, why the exponent τ' is not too far from the value 3/2 corresponding to the distribution of first returns to the origin for the random walk. The difference is probably due to the presence of singular extinctions.

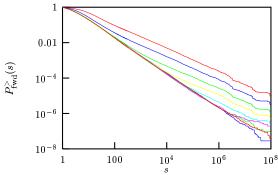


FIG. 4. Distribution of forward avalanche sizes, averaged over 12 independent runs. Each run lasted $3 \cdot 10^8$ steps. The values of λ are (from bottom to top) 0.013, 0.016, 0.02, 0.03, 0.05, 0.1, 0.2, 0.4, 0.6. The superscript > indicates that we count all events larger than s.

The fact, that the number of units change, enables us to define the extinction size in a more realistic way than in the previous variants of the BS model. For fixed λ we

count number of units which were present at the beginning of the λ -avalanche and are no more present when the avalanche stops. This quantity corresponds better to the term "extinction size" used by paleontologists than the number of units affected by mutations, as it is defined in the BS model.

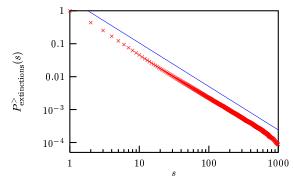


FIG. 5. Distribution of extinction sizes for $\lambda = 0.016$, averaged over 12 independent runs. Each run lasted $3 \cdot 10^8$ steps. The full line corresponds to exponent $\tau_{\rm ext} = 2.32$. The superscript > indicates that we count all events larger than s.

For $\lambda = \lambda_c = 0.016$ the distribution of extinction sizes follows the power law with exponent $\tau_{\rm ext} = 2.32 \pm 0.05$, as is shown in Fig. 5. (The value of the exponent was obtained by fitting the data in the interval (10, 1000).) This value is larger than the exponent 2 observed in the statistics of real biological extinctions, but still closer than the values found in previous modifications of the BS model.

The fact, that the network evolves and the number of units fluctuates leads to significantly larger values of the exponent than in the BS model, even greater that the experimental one, while variants of the BS model have values lower than the experimental one. This suggests, that the freedom in changing the topology in our model is exaggerated and in order to obtain a more realistic model of the biological evolution, we should look for some principles, which imply freezing of the topology, while allowing the species to be replaced by new ones.

We studied several other modifications of our model, in order to check its robustness. For example, the link between "mother" and "daughter" unit was established, or only certain fraction of the links connecting "mother" to its neighbors was inherited by "daughter". These modifications affected some aspects of the network dynamics, but the avalanche and extinction statistics was not significantly different.

To sum up, we formulated and studied the extremal dynamics model derived from the Bak-Sneppen model, which exhibits forward-avalanche exponent close to two, due to the annealed topology of the network. The extinction size was defined in more realistic manner compared to previous approaches within the BS model and the extinction statistics was found to obey a power law with exponent somewhat larger than two. The value found is

closer to paleontological data than in the previous variants of the BS model.

We wish to thank A. Markoš for useful discussions.

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- [25] To establish the error bars δ for the exponent α (which can be τ , τ' or $\tau_{\rm ext}$) we used the following procedure. Let I=(a,b) be the interval, in which α was determined by fitting the data. We choose a moving subinterval $I'=(a',b')\subset I$ with fixed ratio b'/a' and find the value α' of the same exponent by fitting in I'. The error bars are then established by the requirement that $\alpha'\in(\alpha-\delta,\alpha+\delta)$ for any choice of the subinterval I'. For the exponents τ,τ' , we used b'/a'=10, so that I' covers one decade, while for $\tau_{\rm ext}$ we set $b'/a'=\sqrt{10}$.